Chapter 8

General discussion

INTRODUCTION

Life-history theory assumes that individuals behave optimal and hence the reproductive decisions they take should maximize fitness (Lessells 1991; Roff 1992). Optimal reproductive investment involves trading-off both the number versus the quality of offspring produced (Lack 1947) and the current versus the future reproduction of the parent (Charnov & Krebs 1974; Williams 1966). To be adaptive, reproductive decisions may be tuned to environmental factors, including social factors. In wild populations, phenotypic adjustment of reproductive decisions provides a rapid way to respond to spatial and temporal variability of the environment (Stearns 1989). Density dependence of clutch size, ubiquitous in avian populations (Both 2000), is one of the well known examples of reproductive adjustment to environmental factors. Experimental studies showed that negative density dependence of clutch size was a response to an increase of local competition for food prior- or during the nestling phase (e.g. Arcese & Smith 1988; Both 1998b; Nager *et al.* 1997; Soler & Soler 1996 but see Dhondt et al 1992) and this may be adaptive (Both *et al.* 2000). Nevertheless, there is also growing evidence that local density can convey positive information about habitat quality rather than being an indication of competition level. If birds cue on the breeding performance of conspecifics (public information) to make settlement and reproductive decisions, a high local density in one year can indicate high quality habitat in which breeding could enhance fitness the next year (Danchin *et al.* 2001). Therefore, in this thesis we 1) experimentally quantified how social environment (local density and local sex ratio) causally affected the fitness consequences of variation in reproductive choices and 2) determined the spatial scale at which phenotypic selection on individual decisions took place in a single great tit meta-population (*Parus major*). Negative effects of intra-specific competition induced by altered social environment on brood size related fitness were primarily examined but positive effects (e.g. via public information use) were also considered. We also examined the effects of social environment on juvenile redistribution over the study area to unravel the mechanisms underlying variation in individual decision making.

DISCUSSION OF THE GENERAL FINDINGS

The Lauwersmeer great tit population (*Parus major*) is characterized both by an increase of population over time and by a negative density dependence of clutch size between the years. Unlike other studies (Both 1998b; Török & Toth 1988), the decrease of clutch size with density was not caused by an increase of competition for food during the nestling phase and was the result of individual adjustment rather than the result of selection (chapter 2). If the decrease of clutch size over time was caused by a density effect the birds must have adjusted their clutch size to competition experienced at a scale much larger than the area where they collect food for the young (e.g. competition for food in early spring or competition for space after fledging).

I will summarize in the next paragraphs the main findings regarding causal effects of altered social environment on habitat choice and reproductive trade-offs and will discuss their implications for further studies.

Dispersal and habitat selection

Whether to disperse and where to go are the first important decisions a fledged bird has to take in its early life and therefore individuals are expected to be under selective pressures to make optimal settlement choices (Fretwell & Lucas 1970; Kristan 2007). Yet, on which basis juveniles take these decisions is still largely unknown. Besides the intrinsic quality of the environment, discrimination among possible suitable habitats may be greatly influenced by their social environment (e.g. local densities). The presence of other individuals in a habitat may elicit competition for limited resources and aggression among settlers, implying that individual fitness in a habitat is density dependent (Fretwell 1972). We may thus expect that juvenile settlement decisions will be driven by the avoidance of competition. On the other hand, there are many cases where individuals prefer to settle close to conspecifics (Stamps 1988). This may occur when individuals monitor other's interactions with the environment to gain knowledge about possible suitable breeding habitats (Danchin *et al.* 2004). Social information inadvertently provided by other individuals may be used to localise available resources in the habitat (social attraction) or to assess the quality of the habitat (public information) (Valone 2007; Valone 1989). Public information can be accessed through the local breeding performance of hetero- or conspecifics that share similar requirements (see review in Danchin *et al.* 2001). If public information is used, individuals would settle close to successful breeders to benefit from the same favourable conditions. Yet use of public information is expected to be counterbalanced by competition. If all individuals of a population make similar choices, habitat quality will deteriorate due to increased local density (Doligez *et al.* 2003) and raised competition (Courchamp, Clutton-Brock & Grenfell 1999).

In this thesis, the mechanisms underlying the dispersal and settlement decisions of juvenile great tits were examined with the focus on these two opposite processes, competition avoidance and the use of public information. In this species, individuals can express territorial behaviour at the onset of the first autumn following fledging (Drent 1984). In our study the fledglings reduced their post-fledgling movements on average within a month (Michler *et al.* unpublished) indicating that settlement decisions occurred in an earlier phase, i.e. just after fledging. We studied how an experimentally altered social environment experienced by birds during the critical period after fledging affected their post-fledgling movements and settlement decisions. We examined whether increased fledging density and increased sex ratio (male biased plots) were unattractive (competition avoidance hypothesis) or attractive (public information hypothesis) and whether this effect differed between the sexes.

Female juveniles dispersed and settled further from their natal plots than males (chapter 5 and box C), as reported before in this species (Greenwood *et al.* 1979). Females may have avoided competition for food with males during the post-fledging

period (Fig 8.1-8.G; box C). Overall, natural plot nestling density had a strong negative effect on yearling habitat selection. Birds were more likely to emigrate from high density plots and less likely to settle in such high density plots, especially males (chapter 5, Fig. 8.1-7.F. and 8.1-9.F), the latter effect being perhaps the consequence of permanent emigration from these plots. Juveniles may have left natural high density plots after fledging and never return back in these areas the next spring. Our findings were consistent with the 'competition view' where high local density enhanced competition for local resources especially competition for territories and prevented juveniles from settling in these habitats (e.g. Delestrade *et al.* 1996; Krebs 1971; Nilsson 1989; Fig. 2). Whether juveniles actively avoided these high competitive environments as a means to increase fitness or whether they were forced to leave because they were out-competed by prior resident birds is still unknown (Krebs 1982; Sandell & Smith 1991).

Interestingly, habitat choice was also affected by the plot sex ratio manipulation such that juveniles settled preferentially in plots that were male biased the previous year (Fig. 8.1-9.G; chapter 5). This result was in agreement with the 'public information' hypothesis. High juvenile densities resulting from philopatric behavior of these males rather than high proportions of males per se may have signaled good quality habitat to prospecting young in the summer (Doligez *et al.* 2002; Doligez *et al.* 2008; Fig. 2). This effect can also explain why juveniles fledged in increased fledging density plots dispersed less far during the post-fledging phase (Fig. 8.1-8.E; box C). A similar mechanism was found for adult collared flycatchers (*Ficedula albicollis*) of which immigration and emigration decisions were based on conspecific breeding performance in terms of apparent breeding success (i.e. fledging density) and/or condition of young produced (Doligez *et al.* 2002; Doligez *et al.* 2004). In collared flycatchers and in blue tits (*Cyanistes caeruleus*), juvenile habitat choice was also negatively affected by intra- or inter-specific competition (Doligez *et al.* 2004; Parejo *et al.* 2007) consistent with our findings. An alternatively explanation for the increased settlement in the male biased plots is that adult survival with enlarged broods was lower in male biased environments (chapter 6 discussed in the following section). Their disappearance may have provided vacancies allowing more juveniles to settle in male biased plots.

Our study provides experimental evidence that the local social environment during the summer plays an important role in the redistribution of juveniles over the habitat the next year and is a key-factor in understanding population dynamics. Both the use of social information and intra-specific competition are important to understand the decision to leave and the decision to settle (Fig. 8.2). The predominance of one of the two mechanisms (use of public information vs. competition) in explaining dispersal and settlement patterns of juveniles will depend on the ecological settings in the local environment (e.g. overall level of competition for resources), the time during which public information is available (e.g. shorter period of time for migratory species), the individual features (e.g. competitive abilities) and the ability of juveniles to gather this information (e.g. flocking behaviour of juveniles in tit species may facilitate this process).

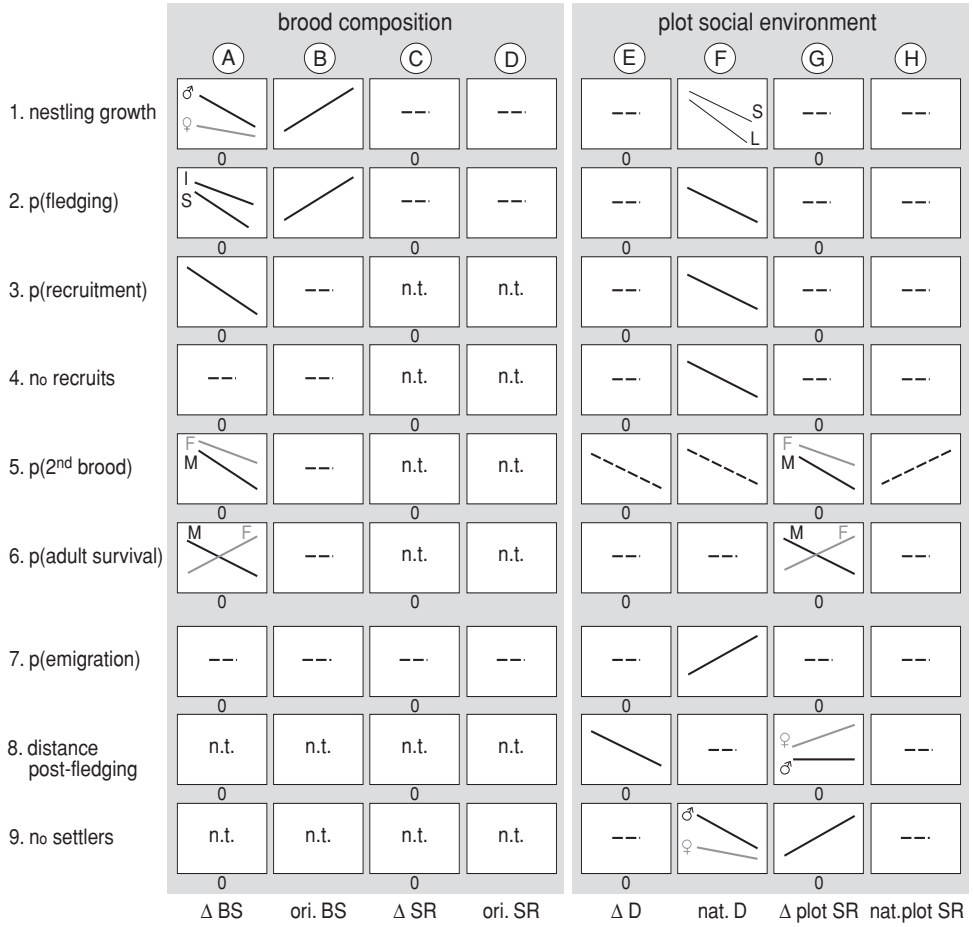

Figure 8.1 Overview of the effects of the social factors at a brood and a plot level on the different fitness components studied in this thesis (chapters 3-6, box C) in 2005, 2006 and 2007 in the Lauwersmeer great tit population. Positive or negative dashed lines indicate trends while flat short dashed lines indicate the absence of effects.

Juveniles should select the habitat that will maximize their fitness. Because the habitat selection process is affected by the local social environment of these young, their subsequent reproductive decisions are expected to be influenced by these social effects as well. Young great tit social environments in the nest or in the fledging plot could for instance induce physiological changes that influence individual reproductive capacities. Different individual histories may then underlie variation in laying date or clutch size. Alternatively but not exclusively, social effects on reproductive decisions may work after settlement because the redistribution of juveniles over the

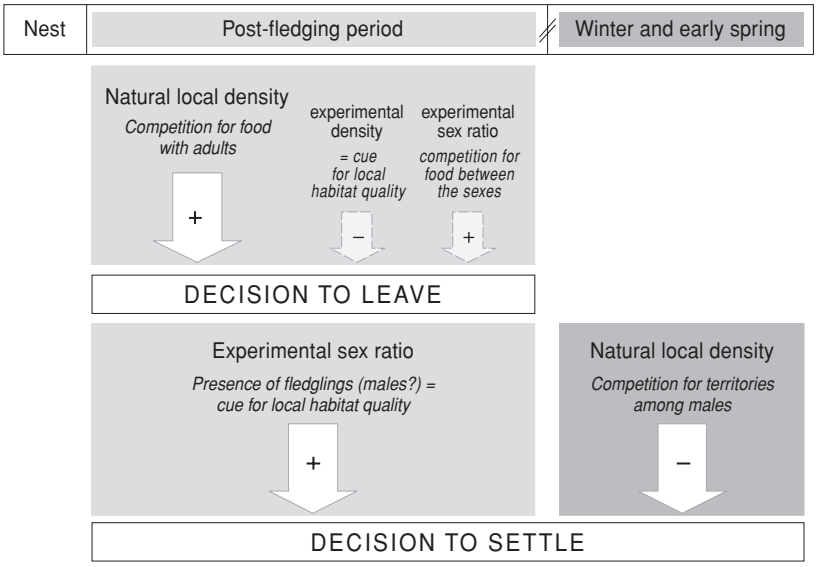

Figure 8.2 Overview of the social factors involved in emigration and immigration decisions of juvenile great tits in the Lauwersmeer population over time (summary of effects found in chapter 5 and box C). The mechanisms supposed to be involved in these processes are indicated in italics. Dashed arrows and grey text summarized the preliminary results found in the study of post-fledging movements (box C).

area creates new local environments that birds may use to tune their breeding decisions on (see also Fig. 8.3). Furthermore, by manipulating local social environments we altered the reliability of the social information that juveniles used for taking dispersal decisions. That implies that juveniles may have been tricked and consequently may not have been able to make the best possible choice. If they did not readjust their breeding decisions to the local conditions in the next spring, their breeding performance may be worse than other birds in the plot. This hypothesis should be further investigated. In the next section we will discuss the social effects on reproductive trade-offs.

Reproductive decisions

Once individuals have settled and mated, they face the decision on how many offspring to produce. During this phase when birds are confined to small areas, we expect a high local density to generate a high level of competition and thereby to affect brood size related fitness negatively. Because the sexes are equally expensive to raise for the parents (see discussion below) but male is the dominant sex (Hogstad 1989), a high local proportion of males is expected to elicit a high level of competition once juveniles have fledged and start competing with the adults. In our study, the effect of altered competition on fitness costs and benefits of brood size can work via (1) brood size related competition among parents in the plot and among

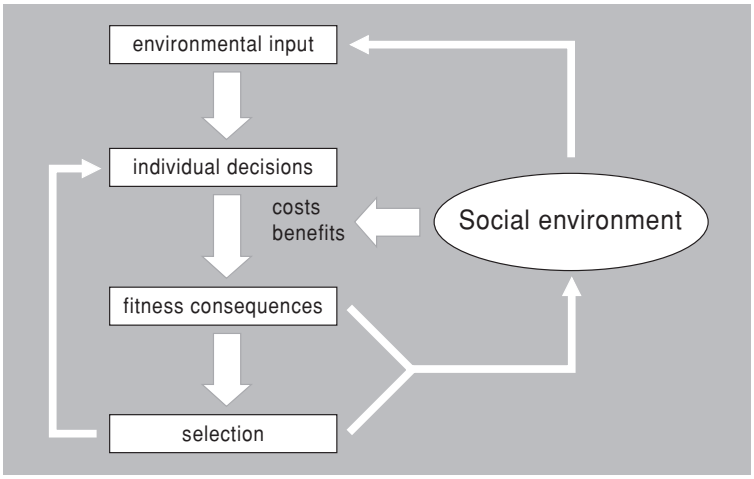

Figure 8.3 Overview of the implications of local social environment for local adaptation process and population dynamics: individuals take reproductive decisions (e.g. clutch size or settlement decision) shaped by selection and adjusted to the environmental circumstances (e.g. food situation). The local social environment (e.g. local density or sex ratio) where these individuals breed affects the fitness costs and benefits of their choices and its subsequent fitness consequences. New social environments will then be created as a result of natural selection (e.g. through selective morality or non-random dispersal) that will influence the environmental outputs used by birds to take reproductive decisions the next year.

nestlings in the nestling period (2) competition for resources (food, mates or territory) among parents and yearlings in the plot after fledging. For both periods we quantified the causal effects of competition on reproductive trade-offs. The general expectation was that the fitness costs associated with large broods are higher in high competitive environments (high density and / or male biased plots). Because females are subordinate to males they may be more negatively affected by a high proportion of surrounding males if competition between the sexes is important. If competition with the sexes is important, the rarer sex is expected to enjoy higher fitness.

Nestling phase

Consistently with theoretical expectations (Lack 1947) and most empirical studies (see reviews in Dijkstra *et al.* 1990; Parejo & Danchin 2006), brood enlargement increased the number of young fledged to the detriment of their quality (Fig. 8.1-1.A, chapter 3). There were no effects of brood sex ratio on growth and nest survival (Fig. 8.1-1.C and 8.1-2.C), showing that nestling males were not more costly to raise (Slagsvold *et al.* 1986) or did not benefit from a competitive advantage over females (Oddie 2000). The negative effect of brood size enlargement on nestling growth was stronger for males resulting in smaller sexual size dimorphism (SSD) in enlarged broods (Fig. 8.1-1.A). Under intensified levels of sibling competition, mortality may have been biased towards the chicks in poorer condition (which may have been the

smallest females) explaining the decrease in SSD. Alternatively, nestling sexes may adopt different strategies in the allocation of limited resources under stressful conditions (Dubiec *et al.* 2006; Tschirren *et al.* 2003). Chapter 3 also revealed that natural traits of both the original and the foster parents were associated with nestling growth, leaving scope for maternal effects, early environmental effects and effect of foster parents phenotypic or territory quality to occur. Further analyses should tease these effects apart. The use of the pedigrees in genetic analyses ("animal models") including the swapped nestlings raised by foster parents provide material to disentangle sources of variation (Postma & Charmantier 2007).

The significant interaction between the natural plot densities and the brood size manipulation on nestling performance (Fig. 8.1-1.F; chapter 3) is interesting because it suggests a sharper fitness decrease with brood size under high competition. Although not significant, the experimental effects of plot density on nestling growth and survival were in the same direction (chapter 3). In natural high density plots, competition for food among adults during the chick rearing period may have been higher (which contrasts with previous findings in this population, chapter 2) and in these high density period, it may be beneficial to produce smaller broods in a high competitive environment. In that way parents could produce fewer young of better condition which are relatively more competitive and more likely to recruit (Both, Visser & Verboven 1999).

After fledging

Offspring components of fitness

Surprisingly we found no effects of our experiments on the number of recruits per nest neither at the brood level (brood size manipulation) nor at the plot level (density and sex ratio manipulations) (Fig. 8.1-4.A, 8.1-4.E and 8.1-4.G; chapter 6). Yet, fledglings originated from enlarged broods were less likely to recruit (Fig. 8.1-3.A; chapter 5). In great tits, nestling mass is a predictor for survival and future fitness (Garnett 1981; Monros *et al.* 2002; Tinbergen & Boerlijst 1990). Reduced body mass of fledglings originated from enlarged broods (chapter 3) may explain their lower recruitment chance (as also supported by the results of chapter 4). The increased productivity of enlarged broods may have been counter-balanced by a reduced recruitment probability of those young and may have resulted in an apparent lack of experimental effects of brood size variation on the number of recruits per brood.

One striking result of this experiment lies in the absence of sex-specific effects. We designed the experiment such that competition within and between the sexes should be affected. This means either that our experiment did not affect the sex-specific level of competition or that juveniles moved too quickly after fledging to allow a sex-specific effect. The fact that altered plot sex ratio affected future fecundity (second broods) and survival of parents with increased brood size and also affected juvenile settlement confirms that the manipulation was effective but did not drive sex-specific effects. We might have modified competition for non sex-specific resources such as food during a phase (e.g. post-fledgling) when birds do not express sex-specific

behaviour. Our results highlight the need to know more about what resources birds compete for and when competition occurs. Future studies in our population should aim at gaining more insight about the mechanisms underlying competition.

Parental components of fitness

Giving extra nestlings to rear is expected to increase parental investment into the current reproduction (e.g. Hegner & Wingfield 1987; Sanz & Tinbergen 1999). Consistently our findings showed that parents with enlarged broods fledged successfully extra nestlings (chapter 3), suggesting that parental effort did increase with brood size. Yet, parents did not meet the full energy requirements of enlarged broods because those nestlings were in lower condition and had lower chances of fledging (Fig. 8.1-1.A and 8.1-2.A; Chapter 3). This may be the outcome of parents balancing the offspring demands against their self maintenance (Williams 1966) or of parents being time constrained in their ability to collect food. Quality of the prey item correlates often positively with searching time (e.g. Grieco 2002). Thus when parents have to increase their provisioning effort, they might trade-off the quality of prey collected against their number, bringing more of lower quality prey that are easier to get (Smith *et al.* 1988; Tinbergen 1981). This shift of nestling diet may no longer cover brood energy or nutritional requirements.

Importantly and in contrast to many empirical studies (see reviews in Dijkstra *et al.* 1990; Parejo & Danchin 2006), we found that brood size manipulation did entail reproductive costs. Interestingly, these costs expressed in terms of reduced probability of producing a second brood and adult local survival depended on the proportion of males in the plot, i.e. on the levels of local competition (Fig. 8.1-5.A and 8.1-6.A; chapter 6). Male biased plots were expected to elicit high level of competition both because males are dominant and philopatric (Greenwood *et al.* 1979; Wilson 1992) and consequently more fledglings were expected to remain in these plots. The analysis of local survival of juveniles after fledging confirmed that in 2006 juveniles in male biased and control plots had an apparent higher survival than juveniles in female biased plots which may be explained by a higher philopatric behaviour of birds in these plots (Michler *et al.* unpublished). In addition, this high level of competition may also have been reinforced by the non-random settlement of juveniles that were attracted to male biased plots (chapter 5). Therefore, we propose that the mechanisms involved in the expression of reproductive costs are the following:

Parents with enlarged brood size become of lower phenotypic quality (e.g. lower body mass, Nur 1984; Smith 1988; lower immune response, Pap & Markus 2003; delayed moult, Svensson & Nilsson 1997) because allocating more resources to offspring production implies allocating less to self maintenance. In high competitive environments, parents of reduced phenotypic quality may then be outcompeted by birds in better shape and in the long run pay a higher cost of reproduction (reduced residual reproductive value). The cost of reproduction is thus expressed as an ecological cost.

In female biased plots, the relationship between brood enlargement and adult survival was positive (Fig. 8.1-6.A; chapter 6) which did not support the last reasoning

because this relationship was expected to be also negative but with a less steep slope. Although we do not understand the pattern in female biased plots, we propose that it may perhaps be explained in the following way. In birds, dispersal is often biased towards females and individuals of poor condition (Clobert *et al.* 2001; Tinbergen 2005). Therefore in female biased plots, a large number of juveniles is expected to disperse quickly after fledging especially those from enlarged broods. As a result, these plots will carry relatively few competitors and will relieve parents with enlarged broods from their post-fledging parental duties if the absolute number of fledglings they care of is less (Verhulst & Hut 1996). This may translate into higher survival chance for parents with enlarged broods and lower survival chance for parents with reduced broods.

IMPLICATION FOR OPTIMAL CLUTCH SIZE

Life-history theory states that parents should produce the number of offspring that maximizes their fitness (Roff 1992). Therefore when local circumstances change, birds should adjust their breeding decisions to the environmental factors by the means of phenotypic plasticity. Ecological studies provide evidence for the existence of plastic adjustment of clutch size to extrinsic factors. It has been shown that birds reduced clutch size when population density increases at a local scale (Both 1998a but see Dhondt et al 1992) or at the population scale (chapter 2) or when local food situation changes (Arcese & Smith 1988; Nager *et al.* 1997; Soler & Soler 1996). It was suggested that this adjustment can be adaptive and that optimal clutch size decreased with population density, i.e. with the level of competition for food during the nestling period (Both *et al.* 2000). When the clutch size decision is tuned to the local circumstances and to the phenotypic quality of the birds, it is expected to optimize fitness at an individual level (Perrins & Moss 1975; Pettifor *et al.* 1988). In this thesis we found no evidence that fitness peaked at intermediate brood size and no evidence for individual optimization (chapters 6 and 7) although we detected variation in parental phenotypic or territory quality in period 2 (chapter 7, Fig. 8.1-2.A).

In the box D, we depict the relationship between fitness and brood size in six different situations where the selective forces acting on brood size at a population level are stabilizing or directional in the presence or absence of an effect of bird phenotypic variation in quality and individual optimization. When these scenarios are compared with known studies in the great tit, it appears that stabilizing selection on brood size at a population or individual level is not a general phenomenon (Table 1 in box D). Out of twelve situations summarized, only four showed stabilizing selection at a population level and / or revealed individual optimization (Table 1 in box D). In the rest of the studies, selection on brood size was either directional or fluctuating between years without occurrence of individual optimization. This observation questions the notion of local optimization of reproduction as being a general rule in avian populations. The implications of our findings for optimal brood size will be discussed in the following sections.

The main problem when studying optimization of reproduction is that it is very hard to quantify fitness consequences of brood size for two reasons: Firstly, the unknown fraction of offspring that disperses outside the study area prevents unbiased fitness estimates of brood size manipulation, especially if there is a fitness cost of reproduction to the parents. The clutch size that maximizes individual fitness results from a trade-off between parental fecundity and parental survival (Charnov & Krebs 1974). Therefore overall brood fitness needs to encompass both recruitment of the current brood and adult survival. However, combining these fitness components in one fitness measure is problematic because the rate of dispersal between adults and juveniles differs strongly (Greenwood & Harvey 1982) resulting in an unknown fraction of mainly offspring that leave the area that will bias fitness estimate. Without full knowledge of dispersal, the estimates of fitness are impossible.

Secondly, the existence of fitness costs and benefits associated to clutch or brood size in other reproductive phases (e.g. costs of egg production and / or incubation, de Heij *et al.* 2006; Monaghan & Nager 1997; Visser & Lessells 2001) also prevents unbiased estimates of the fitness consequences of clutch size (see discussion in de Heij *et al.* 2006). Without a complete fitness estimate it is not possible to detect the clutch size that maximizes fitness. That is the reason that I discuss the fitness components (adults and offspring) separately in this thesis.

In chapter 7, we found for period 2 a differential cost of reproduction between the parental sexes such that overall brood enlargement reduced the survival of the males but not of the females. In great tits where parental care is shared between the sexes, a sexual conflict over the brood size to produce may appear if the costs of brood care are higher for males than for females (Trivers 1972). A differential cost of reproduction between the sexes (chapter 7) indicates that the optimal brood size for males may be smaller than for females. Hence a sexual conflict over the number of offspring to produce could result in a compromised brood size that did not optimize individual fitness. The fact that we found no effect of the brood size manipulation on the number of recruits per nest (chapter 6) makes the existence of sexual conflict over brood size unlikely in our study period.

In the Lauwersmeer population selection on brood size was positive in an early period (period 1: 1995-1998) and negative a later period (period 2: 2005-2007) (Chapter 7). Tinbergen and Sanz (2004) proposed that the existence of costs of incubation associated with large clutches could explain why birds produced “too small” clutches in the first period (de Heij *et al.* 2006). Nevertheless this explanation can not explain why birds lay “too large” clutches in the second period. It is usually expected that reproductive trade-offs and costs of reproduction are detected under “bad circumstances” (Lindén & Møller 1989). Therefore, the high costs of reproduction associated with large broods in the second period (chapter 6) indicate that great tits in the Lauwersmeer experienced worse conditions in the current years than 10 years ago. This may have been caused by a degradation of the habitat over time. In support, we observed a decrease in reproductive traits and body size of offspring (chapter 2) and adults (unpublished) between years. We have evidence that local

densities in period 1 did not generate competition for food during the nestling phase (see chapter 2) while it may now play a role (period 2, 2005-2007; a negative effect of natural local densities on nestling growth and survival, chapter 3). A reduction of resources and an increase of breeding density over time may have modified the intensity and the scale of competition and may have affected the selective pressures acting on brood size. Selection on brood size in the same population can thus change over time

Other processes can explain the absence of fitness peak at intermediate brood sizes. If birds use environmental cues to take breeding decisions, any unpredictable variation of the environment could prevent birds to produce the adequate brood size (e.g. Blondel 1998). We do not have quantitative data about environmental components over time such as food or vegetation so we cannot rule out the possibility that bird reproductive decisions did not track changes in the environment. The presence of gene flow that homogenizes the population gene pool may be also another mechanism underlying the lack of local adaptation (Dhondt *et al.* 1990; Postma & Van Noordwijk 2005). In our population, the percentage of immigrants (i.e. non-locally born birds) represented up to 46% of the breeding birds in certain years. Hence the presence of immigrants leaves the opportunity for genetic mixing that could prevent genotypes to respond to selection. Detailed genetic analyzes would be needed to investigate this possibility. Moreover, the brood size manipulations (period 1 or 2, chapter 7) revealed the existence of reproductive trade-offs at a phenotypic level. Yet as discussed by Roff (1992), these findings do not prove that these trade-offs have an evolutionary significance. Variation in brood size may reflect for instance variation in female condition that is uncorrelated with genetic variation (Price & Liou 1989). If true, this would prevent natural selection to operate on this trait because the genetic basis of life-history traits is a requirement for evolution. However, in this population the repeatability and heritability (±se) of clutch size were respectively 0.58 and 0.36±0.16 which indicates that clutch size in our population presented large genetic variation (box A). This leaves scope for natural selection to shape the evolution of brood size in this population.

SOCIAL EFFECTS ON INDIVIDUAL DECISIONS

Of importance for further studies on optimal clutch size, we found that social effects play an important role for the individual decision making process (see scheme in Fig. 8.3). Juvenile emigration and settlement decisions were the outcome of a cascade of events where juveniles balanced use of public information (i.e. positive effect of fledgling density) and avoidance of competition (i.e. negative effect of adult density) (chapter 5). We also showed that local competition affected the cost of reproduction (chapter 6), such that it was beneficial to produce smaller broods in high competitive environments (i.e. in male biased plots) and larger broods in low competitive environments (i.e. female biased plots). The individual decisions on where to settle and

what brood size to produce are interconnected because the attraction of juveniles to male biased plots may have enhanced the competition pressure on parents of lower phenotypic quality (i.e. with enlarged brood size) while in female biased plots the departure of the juveniles may have relaxed the level of competition. Consequently the non-random settlement of juveniles may have reinforced the fitness costs of large broods in competitive environments. Alternatively the adults may have died first leaving more vacancies in male biased plots and allowing more juvenile settlers. If female biased and natural high density plots are considered as source plots (high emigration and low settlement) and male biased plots as sink plots (high settlement), non-random dispersal of juveniles in combination with selective mortality of parents in high competitive environments may be important for both population dynamics and local adaptation process. These processes will indeed modify the local breeding composition of the plots the next year, affecting the local level of competition and influencing individual breeding decisions (Fig. 8.3).

The existence of a differential cost of reproduction between plots of varying social composition showed that local social environment influenced the selective pressures on brood size at a very small scale, i.e. at the scale of a plot. Selection favoured small broods in high competitive environments and large broods in low competitive environments. This leaves scope for a rapid evolutionary differentiation of clutch size at a small spatial scale as found with body mass in the Wytham great tit population (Garant *et al.* 2005). Tinbergen (2005) showed that brood size affected natal dispersal distance and suggested that if clutch size was heritable, local adaptation of clutch size will depend on the spatial heterogeneity of the habitat. The fitness effects of the social environment found in our study bring thus new perspectives for micro-evolutionary processes determining clutch size.

CONCLUDING REMARKS

Our findings highlight several important issues illustrating that social effects can play an important role in micro-evolutionary processes determining clutch size:

1. Local social environment affected the cost of reproduction consequently optimal clutch sizes may depend on the social environment.
2. Local social environment affected the settlement decisions of juveniles, both as a cue for high quality habitat and as a predictor for high competition.
3. The cost of reproduction differed between the sexes potentially resulting in a sexual conflict over reproduction.
4. The direction of selection can change dramatically over time. Reproductive decisions of birds may not track the environment when resources and competition are changing over time and where a lot of genetic mixing is occurring.
5. When dispersal is not fully known, estimate of the fitness consequences of clutch size variation is impossible. This is why we quantified the consequences of brood size manipulation on components of fitness.

Box D

Phenotypic selection on brood size: from population to individual level

Marion Nicolaus

INTRODUCTION

The population mean of phenotypic traits can change due to natural selection ((dis-) appearance of phenotypes) or due to phenotypic plasticity (within-individual changes), the latter being also under the influence of natural selection. Considering both levels (within- and between-individuals) at which selection pressures may exert their influence on life-history traits is important to understand micro-evolutionary processes.

Avian clutch size has been the subject of numerous investigations because it is a phenotypic trait that presents variation and is partly under genetic control which leaves scope for the action of natural selection (Postma & van Noordwijk 2005). By experimentally altering the parental breeding choice, it becomes possible to quantify the fitness consequences of variation in this trait and to investigate the action of selection at an individual and a population level. From life-history theory, birds are expected to produce the clutch size that maximizes their fitness (Lessels 1991; Roff 1992) trading-off the quantity of the offspring produced against their quality (Lack 1947) and the investment into the current reproduction against the investment into future reproduction (Charnov & Krebs 1974; Williams 1966). Clutch size may also be individually optimized when it is tuned to the phenotypic quality of the birds and its environmental conditions (Perrins & Moss 1975; Pettifor *et al.* 1988). In this box, we describe six hypothetical situations where selection on brood size differ within- and between-individuals in presence or absence of variation in bird phenotypic "quality". We give an overview the studies that quantified the fitness consequences of clutch size or brood size manipulations in great tits (*Parus major*) (table Box D.1) and relate the findings to one of the most likely situation described in figure Box D.1.

1. Stabilizing selection at a population level (Fig. Box D.1A):

Under stabilizing selection at the population level, it is expected that selection will favour one brood size for which fitness is maximal. If selection on brood size is stable over time, it is then expected that the brood size with higher fitness will be the most common one in the population, resulting in one curve relating brood size and fitness that peaks at the optimal brood size. The fitness consequences of a brood size manipulation in such situation (black arrows) will depend on the original brood size of the parents (black dots).

2. Stabilizing selection at a population level and variation in bird phenotypic quality (Fig. Box D.1B):

If individual of the same population differ in their phenotypic quality (including their territory quality) so that some birds can be considered as "good" or " bad" quality, under stabilizing selection, we expect the fitness-brood size curve to differ among birds of different quality. In that case, the brood that maximizes fitness will remain the same for every individual but for similar brood size "low quality" breed-

ers are expected to have lower fitness than "high quality" breeders. As in situation A, the fitness consequences of a brood size manipulation in such situation will depend on the original brood size of the parents (black dots and arrows).

3. Stabilizing selection at a the individual level (Fig. Box D.1C and 1F)

In the situation where selection is stabilizing at the individual level, we expect birds of different phenotypic quality to have different optimal brood sizes so that fitness should be maximized at smaller brood size for low quality breeders than for high quality breeders. In that case, any deviation from the original brood size of the birds should result in lower fitness because birds should produce a brood size that is tuned to their phenotypic quality and their local environment (black dots and arrows). The fitness associated with these optima may depend on the phenotypic quality of the birds (situation C) or may be equal among all individuals (situation F). Whether the selection at the population level will favour one particular brood size depends on the parameter responsible for the phenotypic variation among birds. E.g; if competitiveness is the factor underlying quality variation, high quality birds may spread in the population and therefore selection at the population may be stabilizing on large broods (situation C). If territory quality is the factor underlying quality variation and if the numbers of high quality territories are limited, only fewer birds would occupy them and the most common brood size that may be selected at the population level will be smaller.

4. Directional selection at the population level (Fig. Box D.1D):

If selection on brood size is directional at a population level (e.g. positive or negative), we expect the relation between fitness and brood size to be linear without any optimal brood size where fitness would "peak". The fitness consequence of a brood size manipulation is expected then to be the same for any individuals of the population (dots and black arrows). For instance, under positive selection, fitness is expected to be higher for birds with enlarged broods and lower for birds with reduced broods.

5. Directional selection at the population level and variation in bird phenotypic quality (Fig. Box D.1E):

If bird phenotypic quality differs among the members of a same population, we expect for equal brood size the fitness of the "low quality" breeders to be lower than the fitness of the "high quality" breeders. If selection on brood size is directional in this population, the slope of the linear relation between fitness and brood size should differ among birds of different "quality". In case of positive selection on brood size, a brood enlargement will result in higher fitness while a brood reduction will lower fitness and this stronger for high quality breeders than for low quality breeders (dots and black arrows).

Table Box D.1 Overview of the studies that manipulated clutch size during the incubation phase or brood size and measured the fitness consequences of such manipulation in terms of number of recruits, fecundity and survival costs of reproduction in great tits. Conclusions made regarding the existence of individual optimization (IO) and selection on clutch size or brood size at a population level are indicated (=stabilizing selection; + positive directional selection; - negative directional selection). The corresponding scenario depicted in figure Box D.1 is also given. (0 indicate no experimental effect, -, + and ^{2} indicate respectively negative, positive or quadratic effect of brood/clutch size enlargement; 0/+ or 0/- indicate that the experimental effects are found only in some years).

population	exp	manip	age	F	R	Ft	mS	fS	Ft+1	IO	selection	scenario	references
Gotland, SE	BS	- 0 +	2-3	-	^{2}	-	0	0	0	yes	=	C	1
Hoge Veluwe, NL	BS	- 0 +	1-3		^{2}	-	0	0	0	yes	=	C	2, 19, 20
Hoge Veluwe, NL	BS	- 0 +	1-4	0	0	-/0	0	0		no	?	A or B	3
Hoge Veluwe, NL	BS	0 +	2	+	-/0	0		+/0	0	no	?	A or B	4
Lauwersmeer, NL	BS	- 0 +	2	+	+	0	0	0	0	no	+	D	5, 6
Lauwersmeer, NL	BS	- 0 +	6	+	0	-	-	-	0	no	-	E	8
Lauwersmeer, NL	CS	- 0 +		0	0		-/0	-/0	0	no	=	A	7+5
Tartu, E	BS	- 0 +	2	0	^{2}	0	0	+	0	no	+ ?	D or E	9
Vlieland, NL	CS	- 0			0	-	0	0	0	no	-	D	10
Wytham, UK	BS	- 0 +	0		^{2}		0	0	0	yes /no	fluctuating	C or F / A or D	11,12,13 / 14
Revinge, SE	BS	- 0 +	5	+	^{2}	0	-	-		yes	=?	C or F	15, 16, 17
Buunderkamp, NL	BS	- 0 +	2-4		0					no	?	B or E	18

1 Linden 1990; 2 Tinbergen and Daan 1990; 3 Tinbergen and Both 1999; 4 Visser and Lessells 2001; 5 Tinbergen and Sanz 2004; 6 Sanz and Tinbergen 1999; 7 de Heij *et al.* 2006; 8 this thesis; 9 Horak 2003; 10 Verhulst 1995; 11 Perrins and Moss 1975; 12 Pettifor *et al.* 1988; 13 Pettifor *et al.* 2001; 14 Boyce and Perrins 1967; 15 Smith *et al.* 1987, 16 Smith *et al.* 1988, 17 Smith *et al.* 1989, 18 Both *et al.* 1998; 19 Both *et al.* 2000; 20 Tinbergen *et al.* 1987

exp= type of experiment (BS=brood size manipulation or CS=-clutch size manipulation); manip= experimental categories (- reduced 0 control + enlarged); age=age at which chicks were swapped; F=number of fledglings; R=number of recruits, Ft=probability of producing a second brood; mS=adult male survival, fS=female survival; Ft+1=fecundity the next year

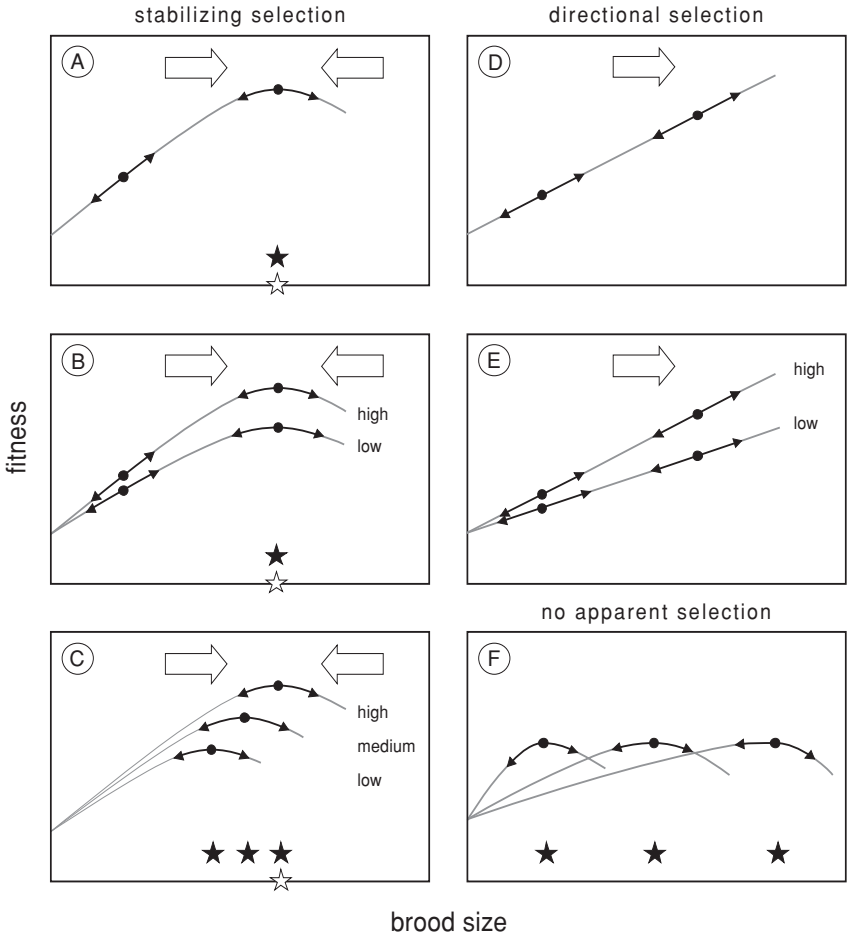

Figure Box D.1 Six hypothetical scenarios for selection on brood size: First stabilizing selection at a population level (A), in the presence of variation in bird phenotypic quality (B), in the presence of stabilizing selection at an individual level (C and F). Second, directional (here positive) on brood size (D), in the presence of variation in bird phenotypic quality (E). Large white arrows indicate the action of selection on brood size at a population level. Black arrows indicate what would be the fitness consequences of a brood size manipulation for a certain brood size (black dots). The stars represent the optimal brood size at a population (white) or individual (black) level.